

Recovery of Oak-Saw Palmetto Scrub after Fire

PAUL A. SCHMALZER and C. ROSS HINKLE

ABSTRACT

We sampled previously established permanent line-intercept transects (15 m length) in oak-saw palmetto scrub 6, 12, 18, 24, and 36 months after a fire and recorded cover by taxon in the 0-0.5 m and >0.5 m height layers to determine patterns of recovery. Transects were located in two stands that were seven years (six transects) and 11 years (four transects) since the last fire when burned. Shrubs and herbs recovered by sprouting with little change in species present or species richness. Regrowth of *Serenoa repens* after burning exceeded that of the oaks; its cover in the >0.5 m layer returned to preburn values within one year. Oak cover (>0.5 m layer) was less than preburn three years after the fire. Differences in growth rates resulted in changes in dominance of mixed oak-saw palmetto transects. We used detrended correspondence analysis ordination to examine resilience after fire. Oak-saw palmetto scrub is very resilient compared to most shrublands. All successional vectors returned toward original locations in fires at 7-11 year intervals. Patterns of recovery varied along the scrub composition gradient. Mixed oak-saw palmetto transects recovered more slowly and showed greater changes in their post-fire composition than saw palmetto-dominated transects three years after burning.

INTRODUCTION

In this paper we describe the response of oak-saw palmetto scrub vegetation to fire. Scrub vegetation is rapidly disappearing (Myers 1990). Some scrub communities support endemic plants now threatened or endangered (Christman and Judd 1990), and oak-dominated scrub is habitat for the Florida Scrub Jay (*Aphelocoma coerulescens coerulescens*) (Woolfenden and Fitzpatrick 1984), listed as threatened by the Fish and Wildlife Service, and for other species of conservation concern (Breininger et al. 1988, Fernald 1989). Management of remaining scrub vegetation is critical to the survival of a host of species. Scrub is a fire-maintained vegetation. Due to the fragmented state of most scrub landscapes, natural fires no longer occur with presettlement size and frequency, and prescribed burning is required to maintain scrub communities (Myers 1990). Understanding changes in scrub composition and structure after fire throughout its range is important to management decisions.

Scrub vegetation in Florida and adjacent states, broadly defined, is a xerophytic shrub community dominated by evergreen oaks or Florida rosemary (*Ceratiola ericoides*), with or without a pine overstory, occupying well-drained infertile, sandy soils (Myers 1990). Some authors (e.g., Laessle 1942) have restricted the term scrub to communities with a sand pine (*Pinus clausa*) canopy and

termed related communities scrubby flatwoods (Laessle 1942, Abrahamson et al. 1984, Abrahamson and Hartnett 1990), while others (Kurz 1942) have used scrub more broadly based on shrub layer composition. A number of scrub types can be recognized based on dominant species (Duever 1983, Myers 1990). Scrub communities are related along depth to water table gradients and differing fire frequencies (Myers 1990) and may grade imperceptibly into flatwoods (Abrahamson and Hartnett 1990, Myers 1990). Myers (1990) noted three major geographic groupings of scrub in Florida: inland peninsula, coastal peninsula, and coastal Panhandle.

Oak-saw palmetto (*Serenoa repens*) scrub vegetation is a scrub type dominated by evergreen, sclerophyllous oaks including *Quercus myrtifolia*, *Quercus chapmanii*, and *Quercus geminata*, *Serenoa repens*, and ericaceous shrubs (e.g., *Lyonia fruticosa*, *L. lucida*) and lacking a pine canopy (Schmalzer and Hinkle 1987). It is generally similar to scrubby flatwoods at Archbold Biological Station (Abrahamson et al. 1984) and elsewhere (Abrahamson and Hartnett 1990). Oak-saw palmetto scrub occupies significant areas on John F. Kennedy Space Center (KSC) (Provancha et al. 1986), where it and associated vegetation types support the largest remaining population of the Florida Scrub Jay (Breininger 1989).

Scrub vegetation is fire-adapted and fire-maintained. The oaks, ericads, and palmettos all resprout after fire (Webber 1935, Abrahamson 1984a, 1984b), while sand pine (Webber 1935) and Florida rosemary (Johnson 1982) are obligate seeding species. Recovery after fire in oak-saw palmetto scrub has been described from an age sequence of stands on similar sites (Schmalzer and Hinkle 1987). The use of data from permanent transects or plots sampled repeatedly after fire has the advantage of directly determining temporal changes rather than drawing inferences from spatial variation (Mueller-Dombois and Ellenberg 1974, Austin 1977). Abrahamson (1984a, 1984b) presented such data for scrubby flatwoods after fire, as have Johnson and Abrahamson (1990) for rosemary scrub. Several studies have followed changes in scrub vegetation in permanent samples in the absence of fire (Veno 1976, Givens et al. 1984, Myers 1985, Menges 1990). These previous studies have all been in inland peninsula scrubs. Here we present data from permanent transects for three years after fire in oak-saw palmetto scrub from a coastal peninsula site.

The resilience of an ecosystem refers to the pace, manner, and degree of recovery of structure and function after disturbance (Westman 1978, 1985; Westman and O'Leary 1986). Components of resilience include: elasticity, the rate of recovery from disturbance; amplitude, the threshold beyond which recovery to the original state no longer occurs; malleability, the extent of alteration of the new stable state from the original; and damping, the extent and duration of oscillation in an ecosystem parameter after disturbance (Westman 1978, 1985; Westman and O'Leary 1986; Malanson and Trabaud 1987). Inertia refers to the resistance to change (Westman 1978). Scrub is considered highly resilient after fire (Abrahamson 1984a, Myers 1990). Here we use ordination techniques (Westman and O'Leary 1986, Malanson and Trabaud 1987) to examine some of the components of resilience after fire and their variability along a scrub environmental gradient.

STUDY AREA

The study site is an inland area on the central part of KSC on Merritt Island on the east coast of central Florida (28°38'N, 80°42'W). Merritt Island has a warm, humid climate. Annual precipitation averages 131 cm, but year-to-year variability is high. Precipitation varies seasonally with a wet season occurring from May to October and the rest of the year being relatively dry (Mailander 1990). Thunderstorms are frequent in the summer months and lightning strikes are common (Eastern Space and Missile Center 1989). Moisture deficits typically occur between mid-March and mid-May and between mid-November and mid-December (Mailander 1990). Mean daily maximum temperatures are 22.3°C for January and 33.3°C for July; mean daily minimum temperatures are 9.6°C for January and 21.9°C for August (Mailander 1990).

The sites occur primarily on Pomello sand (Arenic Haplohumod), a moderately well-drained soil; some occur on the poorly-drained Immokalee (Arenic Haplaquod) or Myakka sand (Aeric Haplaquod; Huckle et al. 1974). These scrub soils are oligotrophic with much of the nutrient standing crops in living and dead vegetation and litter rather than in the mineral soil (Schmalzer and Hinkle 1987).

METHODS

We randomly established and sampled six permanent vegetation transects (15 m length) in each of four scrub stands in January 1983 and resampled them in January 1985 in the absence of fire (Schmalzer and Hinkle 1987). Scrub stands were originally selected to represent an age sequence (2, 4, 8, and 24 years since burning) on otherwise similar sites. In December 1986 a prescribed fire burned through scrub Stands 1 and 2 which were then 11 and 7 years since burning, respectively. In Stand 1, four of six transects burned, and in Stand 2, all six transects burned. We sampled vegetation of the 10 burned transects at 6, 12, 18, 24, and 36 months after fire. We recorded cover of shrubs and herbs by taxon in two height layers, 0–0.5 m and >0.5 m, using line-intercept techniques (Mueller-Dombois and Ellenberg 1974) and measured height of the vegetation canopy above the ground at four points (0, 5, 10, and 15 m from the starting point) along each transect. Sampling methods used were the same before and after the fire. Percent cover by species was calculated as the total cover for a species divided by the transect length (15 m).

Previous analysis (Schmalzer and Hinkle 1987) indicated that composition of this scrub varied along a gradient closely related to depth to the water table with oaks dominating drier sites and saw palmetto increasingly important on wetter sites. Two transects in Stand 2 were dominated by saw palmetto and had soil properties more characteristic of slash pine flatwoods than oak scrub but lacked any pine. We summarized species composition data from these transects separately to determine if recovery patterns differed.

We combined vegetation data (percent cover) from the >0.5 m layer for all sampling periods (pre- to 36 months postburn) and used detrended correspondence analysis (DCA) ordination (Hill and Gauch 1980, Gauch 1982) in the CANOCO package (Ter Braak 1988, 1990) to examine the patterns of compositional change. DCA produces a simultaneous ordination of species and samples.

Table 1. Species composition (mean percent cover) of oak-dominated scrub transects (>0.5 m) preburn and through 36 months postburn

| Species | Preburn 1985 N = 8 | 6 Months | 12 Months | 18 Months | 24 Months | 36 Months |
|-----------------------------|--------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| | | Post- burn N = 8 | Post- burn N = 8 | Post- burn N = 8 | Post- burn N = 8 | Post- burn N = 8 |
| <i>Andropogon</i> spp. | 0.0 | 0.0 | 0.0 | 0.0 | 0.09 | 0.0 |
| <i>Aristida stricta</i> | 1.4 | 0.0 | 0.3 | 1.2 | 2.4 | 8.2 |
| <i>Befaria racemosa</i> | 1.5 | 0.0 | 0.3 | 1.3 | 0.6 | 1.8 |
| <i>Galactia elliottii</i> | 0.0 | 0.4 | 0.0 | 0.8 | 0.0 | 0.0 |
| <i>Lyonia fruticosa</i> | 2.9 | 0.2 | 0.3 | 0.7 | 1.1 | 1.9 |
| <i>Lyonia lucida</i> | 15.9 | 0.5 | 2.1 | 3.3 | 7.5 | 12.1 |
| <i>Myrica cerifera</i> | 0.6 | 0.2 | 0.2 | 1.7 | 1.8 | 2.7 |
| <i>Pteridium aquilinum</i> | 0.0 | 0.0 | 0.0 | 0.04 | 0.0 | 0.0 |
| <i>Quercus chapmanii</i> | 5.2 | 0.0 | 0.8 | 1.2 | 1.4 | 3.1 |
| <i>Quercus geminata</i> | 14.0 | 2.5 | 3.8 | 7.3 | 7.6 | 11.4 |
| <i>Quercus myrtifolia</i> | 33.2 | 1.1 | 1.4 | 7.7 | 9.6 | 17.4 |
| <i>Serenoa repens</i> | 31.5 | 16.8 | 29.3 | 33.4 | 31.1 | 26.5 |
| <i>Smilax auriculata</i> | 0.0 | 0.04 | 0.0 | 0.0 | 0.04 | 0.0 |
| <i>Vaccinium myrsinites</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 |
| Total cover | 106.1 | 21.8 | 38.4 | 58.5 | 63.2 | 85.1 |

We used the option in CANOCO to make all the postburn samples passive. Passive samples have no influence on the extraction of the ordination axes but are added afterward using transition formulae (Ter Braak 1988). Thus, the structure of the ordination was determined by the preburn (1985) samples only, and the postburn samples were located relative to them. Ordination techniques have been used previously to study vegetation dynamics (Austin 1977, Whittaker and Woodwell 1978, Swaine and Greig-Smith 1980, Menges 1990), and recovery after fire (Hobbs and Gimingham 1984, Westman and O'Leary 1986, Malanson and Trabaud 1987). Patterns of trajectories indicate whether samples return toward their preburn locations or change drastically. We compared vector lengths between preburn and postburn locations in ordination space based on the first two ordination axes (Malanson and Trabaud 1987). In the ordination space defined by the preburn samples, distance between postburn samples and preburn is an index of their similarity. In the more common use of ordination to infer environmental gradients, vegetationally similar samples occur close together and dissimilar apart. Here there is an underlying environmental gradient reflected in the ordination of preburn samples. Postburn samples reflect vegetation changes caused by fire and subsequent recovery. Similarity then is an index of change and recovery.

RESULTS

Before burning, *Quercus myrtifolia* had the greatest percent cover in the >0.5 m layer in the oak-dominated transects (Table 1) with *Serenoa repens* second. By one year after burning, *Serenoa repens* reestablished preburn cover

Table 2. Species composition (mean percent cover) of oak-dominated scrub transects (<0.5 m) preburn and through 36 months postburn

| Species | Preburn 1985 N = 8 | 6 Months | 12 Months | 18 Months | 24 Months | 36 Months |
|-----------------------------|--------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| | | Post- burn N = 8 | Post- burn N = 8 | Post- burn N = 8 | Post- burn N = 8 | Post- burn N = 8 |
| Bare ground | 0.0 | 22.9 | 14.6 | 6.1 | 4.9 | 0.7 |
| <i>Andropogon</i> spp. | 0.0 | 0.0 | 0.0 | 0.04 | 0.04 | 0.08 |
| <i>Aristida stricta</i> | 2.7 | 2.8 | 4.7 | 4.0 | 4.0 | 7.2 |
| <i>Befaria racemosa</i> | 0.3 | 0.7 | 1.2 | 0.8 | 1.1 | 1.0 |
| <i>Carphephorus</i> spp. | 0.0 | 0.4 | 0.6 | 1.0 | 0.6 | 0.7 |
| <i>Drosera</i> sp. | 0.0 | 0.0 | 0.04 | 0.0 | 0.04 | 0.04 |
| <i>Galactia elliotii</i> | 0.0 | 1.3 | 0.0 | 1.5 | 0.0 | 0.0 |
| <i>Gaylussacia dumosa</i> | 0.0 | 0.6 | 0.9 | 0.7 | 0.3 | 0.6 |
| <i>Hypericum reductum</i> | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Licania michauxii</i> | 0.0 | 0.04 | 0.04 | 0.04 | 0.0 | 0.0 |
| <i>Lyonia fruticosa</i> | 0.5 | 1.3 | 1.8 | 1.5 | 1.6 | 1.4 |
| <i>Lyonia lucida</i> | 1.7 | 9.7 | 11.7 | 11.2 | 6.5 | 6.3 |
| <i>Myrica cerifera</i> | 1.3 | 3.0 | 2.4 | 2.2 | 2.4 | 3.6 |
| <i>Panicum</i> spp. | 0.0 | 0.04 | 0.08 | 0.08 | 0.4 | 0.5 |
| <i>Pteridium aquilinum</i> | 0.0 | 0.5 | 0.0 | 0.9 | 0.0 | 0.0 |
| <i>Quercus chapmanii</i> | 1.5 | 4.3 | 3.4 | 4.4 | 4.8 | 3.9 |
| <i>Quercus geminata</i> | 1.3 | 9.2 | 6.8 | 6.6 | 4.0 | 5.1 |
| <i>Quercus myrtifolia</i> | 2.8 | 16.6 | 17.0 | 19.9 | 17.8 | 15.4 |
| <i>Serenoa repens</i> | 0.3 | 1.2 | 1.1 | 0.7 | 1.3 | 1.2 |
| <i>Seymeria pectinata</i> | 0.0 | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 |
| <i>Smilax auriculata</i> | 0.1 | 0.09 | 0.08 | 0.08 | 0.0 | 0.0 |
| <i>Vaccinium myrsinites</i> | 1.5 | 2.3 | 2.4 | 3.0 | 3.0 | 3.6 |
| <i>Vaccinium stamineum</i> | 0.0 | 0.09 | 0.0 | 0.2 | 0.0 | 0.0 |
| Total cover | 14.1 | 54.0 | 54.1 | 59.4 | 47.8 | 50.5 |

in the >0.5 m layer. *Quercus myrtifolia* cover in the >0.5 m layer was less than half its preburn value three years after the fire (Table 1). *Quercus myrtifolia* was not eliminated from the stands by fire; cover in the <0.5 m layer increased (Table 2) and was still elevated three years postburn. Cover of *Quercus geminata* reestablished more quickly than *Quercus myrtifolia*; after three years, cover of *Quercus geminata* (>0.5 m) was 81.4% of its preburn cover, while cover of *Quercus myrtifolia* was 52.4% of preburn (Table 1). Total oak cover (>0.5 m) three years postburn (31.9%) was still substantially less than preburn (52.4%). Through two years postburn, *Serenoa repens* cover in the >0.5 m layer exceeded the sum of the cover of all oak species. Saw palmetto cover (>0.5 m) as a fraction of total cover increased from preburn (29.7%) to six months (77.1%) postburn and then gradually declined (12 months—76.3%, 18 months—57.1%, 24 months—49.2%), approaching the preburn proportion at 36 months (31.1%) postburn. *Lyonia lucida* cover in the >0.5 m layer three years after fire was close to preburn. *Myrica cerifera* increased from preburn values in the <0.5 m layer by six months

Table 3. Species composition (mean percent cover) of saw palmetto-dominated scrub transects (>0.5 m) preburn and through 36 months postburn

| Species | Preburn 1985 N = 2 | 6 Months Post- burn N = 2 | 12 Months Post- burn N = 2 | 18 Months Post- burn N = 2 | 24 Months Post- burn N = 2 | 36 Months Post- burn N = 2 |
|---------------------------------|--------------------------|---------------------------------------|--|--|--|--|
| | | | | | | |
| <i>Aristida stricta</i> | 0.4 | 0.0 | 0.0 | 0.4 | 1.0 | 1.7 |
| <i>Befaria racemosa</i> | 1.7 | 0.0 | 0.7 | 0.0 | 0.9 | 2.4 |
| <i>Eupatorium rotundifolium</i> | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Galactia elliottii</i> | 0.0 | 0.7 | 0.0 | 1.5 | 0.0 | 0.0 |
| <i>Ilex glabra</i> | 13.7 | 0.0 | 1.9 | 3.0 | 8.7 | 14.3 |
| <i>Lyonia lucida</i> | 7.0 | 2.0 | 4.0 | 3.0 | 12.8 | 14.5 |
| <i>Myrica cerifera</i> | 3.7 | 0.0 | 0.0 | 0.2 | 0.4 | 2.4 |
| <i>Persea borbonia</i> | 2.0 | 0.0 | 0.4 | 1.0 | 0.7 | 1.4 |
| <i>Pteridium aquilinum</i> | 0.0 | 1.7 | 0.0 | 4.0 | 0.0 | 0.0 |
| <i>Quercus geminata</i> | 1.7 | 0.0 | 0.0 | 1.4 | 1.4 | 0.0 |
| <i>Rhus copallina</i> | 0.0 | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 |
| <i>Serenoa repens</i> | 73.3 | 53.7 | 72.0 | 67.4 | 66.7 | 75.4 |
| Total cover | 103.3 | 58.1 | 78.9 | 82.4 | 92.4 | 111.9 |

and in the >0.5 m layer by 18 months postburn. The subshrubs, *Vaccinium myrsinites* and *Gaylussacia dumosa*, increased in cover in the <0.5 m layer after fire. *Galactia elliottii* and *Pteridium aquilinum* showed a distinctly seasonal response, present in the six and 18 month postburn samples (June) and not in the winter samples. Total cover (sum of the percent cover values of all species) had not returned to preburn levels in the >0.5 m layer three years postburn (Table 1) but exceeded preburn in the <0.5 m layer (Table 2). Percent bare ground declined to near zero by three years after fire (Table 2).

In the saw palmetto-dominated transects, cover of *Serenoa repens* in the >0.5 m layer returned to preburn values within one year; associated shrubs, *Lyonia lucida* and *Ilex glabra*, recovered more slowly but equaled or exceeded preburn cover within three years (Table 3). *Galactia elliottii* and *Pteridium aquilinum* showed the same seasonal pattern as in the oak-dominated transects, present only in the summer samples (Table 4); *Pteridium aquilinum* was much more abundant here than in the oak-dominated transects. Total cover in the >0.5 m layer equaled preburn in three years (Table 3). Percent bare ground declined to near zero by 18 months after fire (Table 4).

Mean vegetation height was still much less than preburn three years after the fire in the oak-dominated transects but had nearly recovered in the saw palmetto transects (Table 5). Species richness (mean number of species per transect) followed similar trends in both groups of transects (Table 5). There were short-term reductions in species richness in the >0.5 m layer and increases in the <0.5 m layer as a result of differential growth rates. Overall species richness generally increased after fire, but the changes were small with considerable variability in species number from transect-to-transect (Schmalzer and Hinkle 1991).

Table 4. Species composition (mean percent cover) of saw palmetto-dominated scrub transects (<0.5 m) preburn and through 36 months postburn

| Species | | | | | | |
|---------------------------------|--------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|
| | 6 | | 12 | | 18 | |
| | Preburn 1985 N = 2 | Months Post- burn N = 2 | Months Post- burn N = 2 | Months Post- burn N = 2 | Months Post- burn N = 2 | Months Post- burn N = 2 |
| Bare ground | 0.0 | 6.5 | 9.0 | 0.5 | 0.4 | 0.0 |
| <i>Andropogon</i> spp. | 0.0 | 0.0 | 0.5 | 0.2 | 1.0 | 0.7 |
| <i>Aristida stricta</i> | 4.7 | 0.5 | 1.4 | 0.5 | 1.0 | 8.7 |
| <i>Befaria racemosa</i> | 0.0 | 2.5 | 1.0 | 0.4 | 0.4 | 0.2 |
| <i>Carphephorus</i> spp. | 0.0 | 0.2 | 0.5 | 1.2 | 0.4 | 0.0 |
| <i>Eupatorium rotundifolium</i> | 0.0 | 0.4 | 0.2 | 1.0 | 0.0 | 0.0 |
| <i>Galactia elliottii</i> | 0.0 | 1.3 | 0.0 | 2.8 | 0.0 | 0.0 |
| <i>Gaylussacia dumosa</i> | 0.0 | 0.0 | 0.2 | 0.7 | 0.0 | 0.0 |
| <i>Hypericum reductum</i> | 0.0 | 0.2 | 0.2 | 0.7 | 0.7 | 0.5 |
| <i>Ilex glabra</i> | 0.4 | 6.0 | 8.4 | 7.9 | 4.9 | 3.2 |
| <i>Lyonia fruticosa</i> | 0.4 | 0.4 | 0.2 | 0.0 | 0.0 | 0.4 |
| <i>Lyonia lucida</i> | 0.4 | 7.3 | 9.2 | 8.0 | 4.4 | 4.9 |
| <i>Myrica cerifera</i> | 0.0 | 6.2 | 5.7 | 7.2 | 7.2 | 8.3 |
| <i>Panicum</i> spp. | 0.0 | 0.0 | 0.9 | 1.9 | 8.0 | 1.8 |
| <i>Pteridium aquilinum</i> | 0.0 | 25.0 | 0.0 | 17.7 | 0.0 | 0.0 |
| <i>Quercus geminata</i> | 0.0 | 0.5 | 0.9 | 1.0 | 0.0 | 0.5 |
| <i>Rhus copallina</i> | 0.0 | 0.5 | 0.0 | 0.4 | 0.0 | 0.0 |
| <i>Serenoa repens</i> | 0.0 | 0.4 | 2.7 | 0.0 | 1.7 | 2.7 |
| Unknown herb | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 |
| <i>Vaccinium myrsinites</i> | 0.0 | 0.7 | 1.4 | 0.0 | 1.4 | 2.2 |
| Total cover | 5.7 | 51.8 | 32.9 | 51.4 | 30.8 | 33.8 |

Table 5. Changes in vegetation height and species richness in oak- and saw palmetto-dominated transects preburn through 36 months postburn

| | 6 | | 12 | | 18 | |
|--|-----------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| | Preburn 1985 | Months Post- burn | Months Post- burn | Months Post- burn | Months Post- burn | Months Post- burn |
| Oak-dominated Transects (N = 8) | | | | | | |
| Height (cm) | 107.9 | 31.8 | 49.8 | 58.4 | 60.2 | 69.6 |
| Species richness (>0.5 m) | 6.8 | 2.8 | 4.0 | 6.4 | 6.3 | 6.6 |
| Species richness (<0.5 m) | 6.6 | 10.0 | 10.1 | 10.5 | 8.5 | 9.5 |
| Species richness (all strata) | 8.5 | 10.5 | 10.4 | 11.1 | 9.9 | 10.1 |
| Saw Palmetto-dominated Transects (N = 2) | | | | | | |
| Height (cm) | 115.0 | 67.5 | 88.0 | 93.6 | 94.0 | 103.3 |
| Species richness (>0.5 m) | 5.5 | 3.0 | 3.0 | 7.0 | 5.5 | 5.0 |
| Species richness (<0.5 m) | 2.0 | 9.5 | 9.5 | 11.0 | 8.5 | 8.0 |
| Species richness (all strata) | 6.0 | 10.0 | 10.0 | 12.5 | 9.5 | 9.0 |

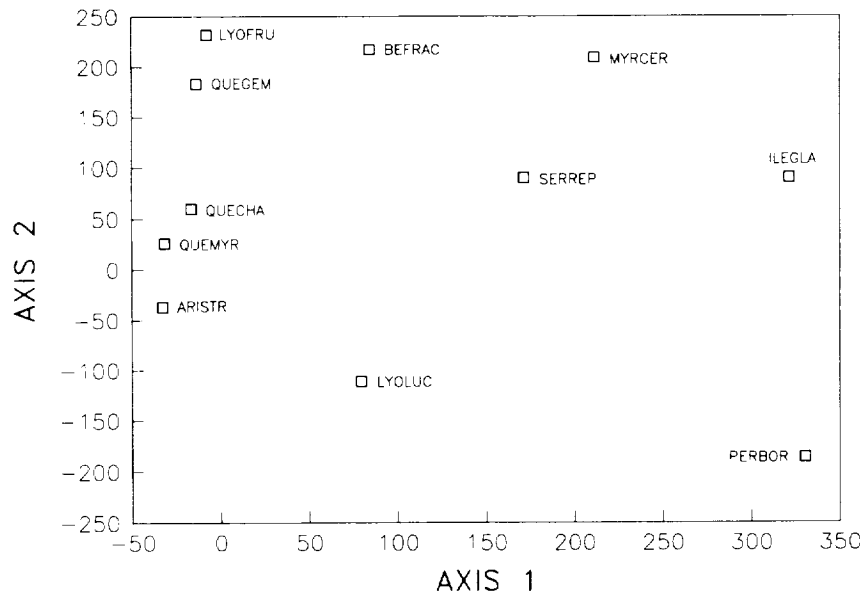


Figure 1. Detrended correspondence analysis species ordination of the >0.5 m layer. Ordination structure was determined by the preburn (1985) samples. Species are: ARISTR, *Aristida stricta*; BEFRAC, *Befaria racemosa*; ILEGLA, *Ilex glabra*; LYOFRU, *Lyonia fruticosa*; LYOLUC, *Lyonia lucida*; MYRCER, *Myrica cerifera*; PERBOR, *Persea borbonia*; QUECHA, *Quercus chapmanii*; QUEGEM, *Quercus geminata*; QUEMYR, *Quercus myrtifolia*; and SERREP, *Serenoa repens*.

The species ordination (Figure 1) placed oak species to the left and saw palmetto and species restricted to the wetter transects (e.g., *Ilex glabra*) to the right on the first axis. In the sample ordination, three patterns of responses occurred (Figures 2–4). These results are from a single ordination but are graphed separately so that overlapping points can be seen. Both saw palmetto transects (P-7, P-8: Figure 2) remained on the right side of the ordination and returned close to their original location by three years after fire. Recovery of saw palmetto transects was rapid; cover and ordination location of Transect 8, 12 months postburn, was similar to preburn. There was a seasonal effect evident in Transect 8 with the six and 18 month postburn (June) samples closely related (Figure 2). Transect 5 (P-5: Figure 3) was oak-dominated with little saw palmetto. It remained on the left of the ordination diagram, returning to near its preburn location by three years postfire. The remaining transects (P-2, P-3, P-4: Figure 3; P-9, P-10, P-11, P-12: Figure 4) were of mixed oak-saw palmetto composition before burning. They all shifted sharply to the right after the fire with subsequent trajectories toward their original locations.

Lengths of the vectors between pre- and postburn locations in ordination space (Table 6) indicate the recovery process. All transects moved toward their

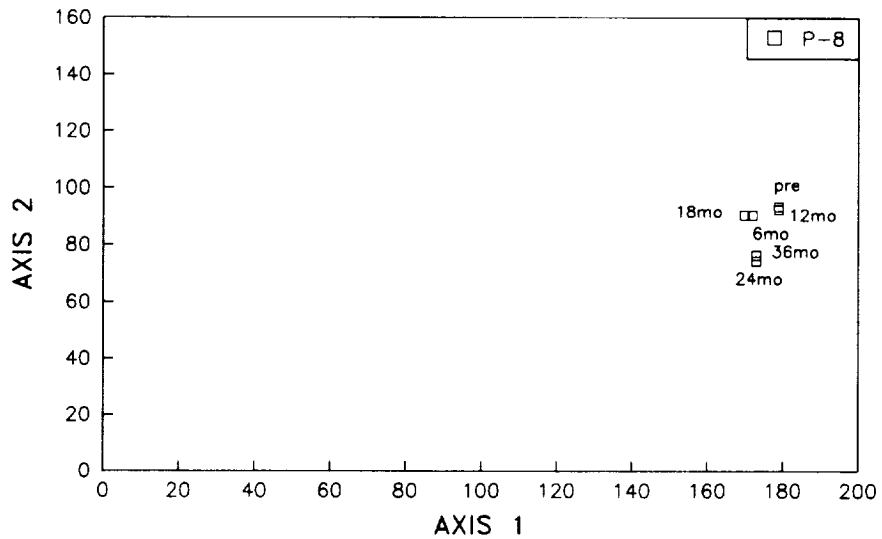
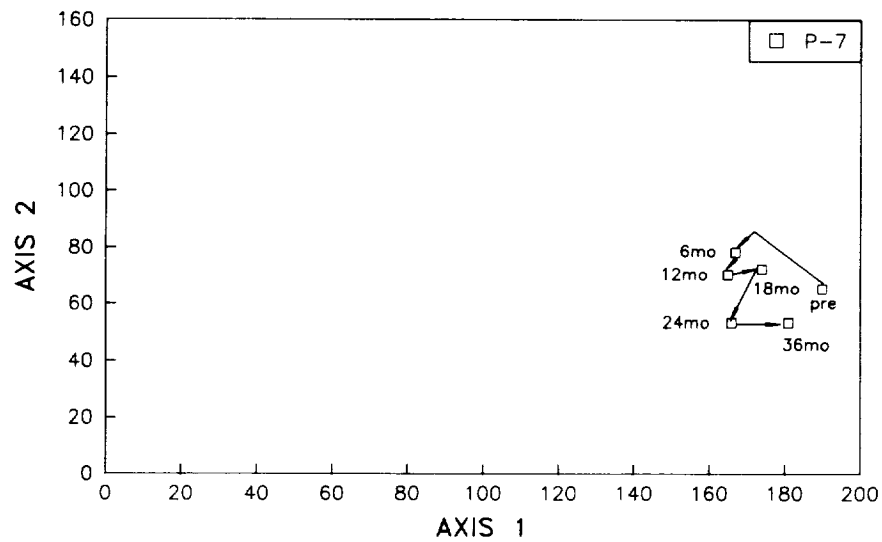


Figure 2. Detrended correspondence analysis sample ordination of the >0.5 m layer showing changes of saw palmetto-dominated transects from preburn through 36 months postburn. Arrows show direction of change. Ordination structure was determined by the preburn samples with postburn samples located passively in relation to them. Shown are transects 7 and 8.

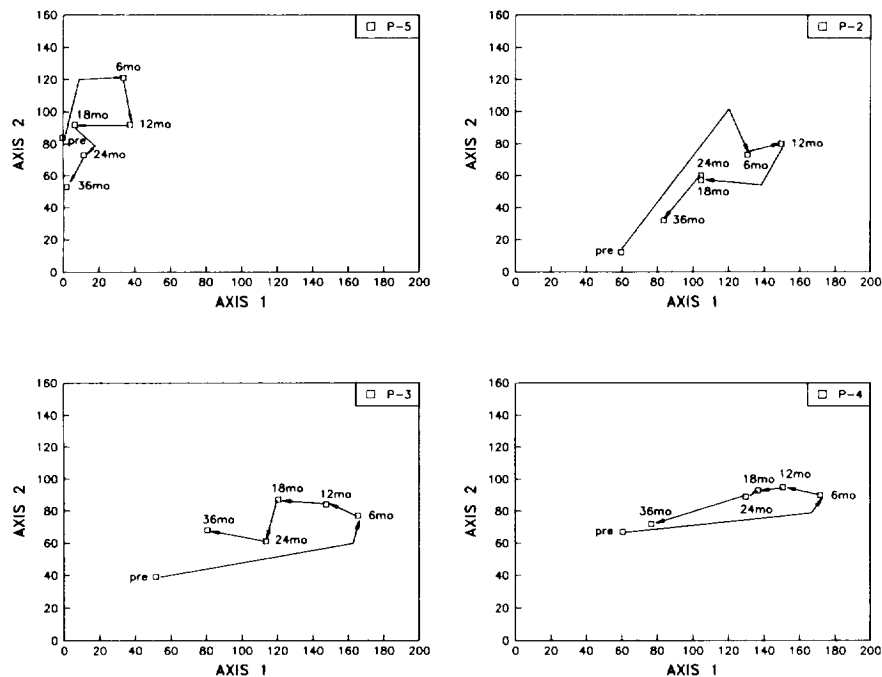


Figure 3. Detrended correspondence analysis sample ordination of the >0.5 m layer showing changes of oak and oak-saw palmetto transects from preburn through 36 months postburn. Arrows show direction of change. Ordination structure was determined by the preburn samples with postburn samples located passively in relation to them. Shown are transects 2, 3, 4, and 5.

original locations. Vector lengths by 36 months were much less than at 6 months postburn (Table 6). Initial postfire (six months) vector lengths were greater for the mixed oak-saw palmetto transects than for those dominated by saw palmetto, indicating a greater degree of change in the mixed oak-saw palmetto transects.

DISCUSSION

Floristic changes in our stands of oak-saw palmetto scrub were minimal with no species lost due to fire and little or no invasion of species not present before burning, agreeing with patterns observed in scrubby flatwoods after fire (Abrahamson 1984a). Many other fire-adapted shrublands exhibit greater floristic changes after fire (e.g., Gill and Groves 1981). All shrub species in our oak-palmetto scrub resprout, as do the perennial forbs and grasses. In many heathlands and mediterranean-climate shrublands there is a range of shrub regeneration patterns from obligate sprouters to obligate seeders (Keeley and Zedler 1978, Gill and Groves 1981, Keeley 1981, Kruger 1983, Christensen 1985). Pocosins (Christensen et al. 1981) and *Quercus coccifera* garrigue (Malanson and Traub 1987) are similar to oak-saw palmetto scrub in degree of dominance by

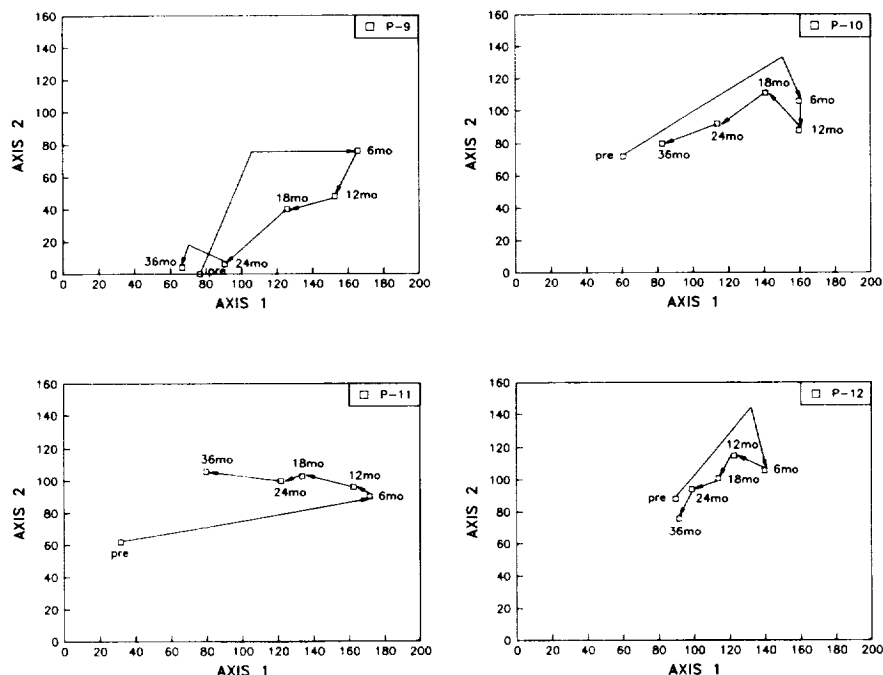


Figure 4. Detrended correspondence analysis sample ordination of the >0.5 m layer showing changes of oak-saw palmetto transects from preburn through 36 months postburn. Arrows show direction of change. Ordination structure was determined by the preburn samples with postburn samples located passively in relation to them. Shown are transects 9, 10, 11, and 12.

sprouting species. Keeley and Zedler (1978) suggested that short fire cycles can eliminate seeder species; this is the case with sand pine (Laessle 1967) and Florida rosemary (Johnson 1982) which can be eliminated by fire cycles of less than about 20 and 10 years, respectively. Scrub shrubs form the understory in sand pine scrub with a 20–70+ year fire cycle (Austin 1976) and are not eliminated by such fire-free intervals (Veno 1976, Givens et al. 1984).

The increase of the subshrubs, *Vaccinium myrsinites* and *Gaylussacia dumosa*, and *Myrica cerifera* in our stands is similar to that reported by Abrahamson (1984b). Here, none of the subshrubs showed a sharp decline in cover by three years postburn. The increases in the cover of grasses (*Andropogon* spp., *Aristida stricta*, *Panicum* spp.) and perennial herbs such as *Carphephorus* spp. are largely due to sprouting. Seedling establishment of herbs such as *Eupatorium rotundifolium* in the wetter transects may have occurred, or these herbs may have been absent at the preburn (winter) sampling times.

Westman and O'Leary (1986) found that coastal sage scrub dominated by vigorous sprouters was more resilient than that dominated by less vigorous sprouters. We expected oak-saw palmetto scrub to be very resilient after fire

Table 6. Lengths of vectors between preburn and postburn location of transects based on first two axes of detrended correspondence analysis ordination

| Transect | 6 Months Postburn | 12 Months Postburn | 18 Months Postburn | 24 Months Postburn | 36 Months Postburn |
|--------------------|----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| 2 | 93.6 | 112.8 | 63.6 | 65.8 | 31.2 |
| 3 | 120.2 | 106.0 | 84.0 | 65.8 | 41.0 |
| 4 | 113.4 | 94.3 | 80.3 | 72.4 | 16.8 |
| 5 | 50.2 | 38.8 | 10.6 | 16.3 | 31.1 |
| 7 | 26.4 | 25.5 | 17.5 | 26.8 | 15.0 |
| 8 | 7.4 | 1.0 | 9.3 | 19.9 | 18.0 |
| 9 | 117.0 | 89.9 | 63.3 | 15.2 | 10.8 |
| 10 | 104.7 | 100.3 | 89.0 | 56.6 | 23.4 |
| 11 | 142.8 | 135.3 | 109.9 | 97.7 | 65.1 |
| 12 | 53.1 | 42.6 | 27.3 | 10.8 | 12.2 |
| \bar{x}_{all}^1 | 82.9 | 74.7 | 55.5 | 44.7 | 26.5 |
| SD_{all}^1 | 45.4 | 44.2 | 36.6 | 30.5 | 16.7 |
| \bar{x}_{sp}^2 | 16.9 | 13.3 | 13.4 | 23.4 | 16.5 |
| SD_{sp}^2 | 13.4 | 17.3 | 5.8 | 4.9 | 2.1 |
| $\bar{x}_{o/sp}^3$ | 106.4 | 97.3 | 73.9 | 54.9 | 28.6 |
| $SD_{o/sp}^3$ | 27.9 | 28.4 | 26.0 | 31.4 | 19.3 |

¹ All transects (N = 10).

² Saw palmetto transects (#7, 8) (N = 2).

³ Oak-saw palmetto transects (#2, 3, 4, 9, 10, 11, 12) (N = 7).

given its dominance by sprouting species. This was the case. All trajectories in ordination space trended back toward the transects' original locations, suggesting that fire occurring seven or 11 years after the preceding burn did not exceed the ability of this community to recover.

Components of resilience are not uniform across the scrub vegetation gradient sampled. After the fire, all transects started as bare ground. Oak-dominated scrub burns less readily than scrub that has substantial saw palmetto cover; thus, the oak-dominated areas have higher inertia (resistance to change) related to fire. Six months after burning, saw palmetto transects were closer to their originating points than mixed transects, suggesting greater elasticity (rate of recovery) in saw palmetto-dominated areas. By three years after fire, none of the transects had reached a stable state. Taking as relative endpoints the three year postburn data, mixed oak-saw palmetto transects have greater malleability (extent of change from original) than saw palmetto-dominated ones. Our sample of oak scrub without saw palmetto was too small for definite conclusions on its resilience. Observations in other oak-dominated areas suggest that they also change little in composition after fire and have low malleability.

It is clear that the differing growth rates of saw palmetto and oaks after fire can interact with varying fire frequencies to modify dominance patterns of sites where these species occur together. Longer fire frequencies will allow oaks sufficient time to reach the >0.5 m layer, but short fire frequencies will enhance saw palmetto dominance.

As Westman (1978) and Westman and O'Leary (1986) have noted, resilience will vary with the parameter measured. In oak-saw palmetto scrub as in *Quercus coccifera* garrigue (Malanson and Trabaud 1987), cover by height layer is a more sensitive indicator of change and recovery than species presence or cover without regard to height, since vertical structure is important to both communities. Mean vegetation height recovered more slowly in oak-dominated than in saw palmetto-dominated transects.

The type of ordination used here was useful in examining recovery of scrub vegetation. Swaine and Grieg-Smith (1980) noted that the success of this approach depends on the changes in the vegetation leading towards species combinations already present in the ordination; this is true with resilient sprouting vegetation like scrub but may be less so with other types. Choice of data set may affect the results as will addition or deletion of samples (Malanson and Trabaud 1987). Using the preburn samples to establish the ordination pattern and relating the postburn samples to them avoids the potentially circular argument that would arise if all the samples were included in the ordination; in addition, the structure of the ordination does not change with the addition of subsequent postburn samples.

The degree of resilience shown here was for a single winter burn after 7–11 fire-free years and should not be extrapolated to other circumstances. Season of burning and fire intensity (Malanson and Trabaud 1987, 1988) can affect resprouting recovery. Growing-season fires generally have a greater impact than dormant-season fires on Florida hardwoods (Robbins and Myers 1990), but data on scrub species are lacking (Myers 1990). Our data suggest that increased fire frequency would increase saw palmetto dominance in areas of mixed composition. Saw palmetto is known for its rapid vegetative recovery after fire (Hough 1965, Hilmon 1968); it is most abundant in communities that have greater fire frequency than scrub or scrubby flatwoods. Saw palmetto requires four years after fire to restore rhizome carbohydrates (Hough 1968); frequent, growing-season fires can reduce root reserves and sprouting in some clonal oaks (e.g., Harrington 1985, 1989). This has not been studied in Florida scrub oaks.

Resilience to fire also does not extend to other disturbances. Mechanical disturbance that damages or removes root and rhizome systems produces long-lasting changes in scrub composition and structure (Breininger and Schmalzer 1990).

Oak-saw palmetto scrub is resilient after fire, but resilience varies along the scrub composition and environmental gradient. Additional work in oak-dominated and saw palmetto-dominated sites could provide useful comparisons to the patterns reported here and lead to better understanding of community responses to differing fire management regimes. Information on the responses of scrub vegetation (e.g., species composition and dominance, vegetation height, percent bare ground) to prescribed fires is important to maintaining conditions appropriate for the plant and animal species dependent on this community.

ACKNOWLEDGMENTS

This study was conducted under NASA contracts NAS10-10285 and NAS10-11624. We thank W.M. Knott III, Chief, Biological Research and Life Support

Office and B. Summerfield, Pollution Control Officer, Biomedical Operations and Research Office, for their support. We thank L. Maull and J. Mailander for field assistance, and O. Tilley and J. Harvey for manuscript preparation. Dr. H.R. DeSelm and several anonymous reviewers provided helpful comments on earlier versions of this paper.

LITERATURE CITED

- ABRAHAMSON, W.G. 1984a. Post-fire recovery of Florida Lake Wales Ridge vegetation. *Amer. J. Bot.* 71:9-21.
- ABRAHAMSON, W.G. 1984b. Species responses to fire on the Florida Lake Wales Ridge. *Amer. J. Bot.* 71:35-43.
- ABRAHAMSON, W.G. and D.C. HARTNETT. 1990. Pine flatwoods and dry prairies. p. 103-149. *In: Myers, R.L. and J.J. Ewel (eds.). Ecosystems of Florida.* University of Central Florida Press, Orlando. 765 p.
- ABRAHAMSON, W.G., A.F. JOHNSON, J.N. LAYNE, and P.A. PERONI. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. *Florida Sci.* 47:209-250.
- AUSTIN, D.F. 1976. Florida scrub. *Florida Naturalist* 49(4):2-5.
- AUSTIN, M.P. 1977. Use of ordination and other multivariate methods to study succession. *Vegetatio* 35:165-175.
- BREININGER, D.R. 1989. A new population estimate for the Florida scrub jay on Merritt Island National Wildlife Refuge. *Florida Field-Naturalist* 17:25-31.
- BREININGER, D.R. and P.A. SCHMALZER. 1990. Effects of fire and disturbance on plants and birds in a Florida oak/palmetto scrub community. *Amer. Midl. Naturalist* 123: 64-74.
- BREININGER, D.R., P.A. SCHMALZER, D.A. RYDENE, and C.R. HINKLE. 1988. Burrow and habitat relationships of the gopher tortoise in coastal scrub and slash pine flatwoods on Merritt Island, Florida. Nongame Wildlife Program Final Report. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida. 238 p.
- CHRISTENSEN, N.L. 1985. Shrubland fire regimes and their evolutionary consequences. p. 85-100. *In: Pickett, S.T.A. and P.S. White (eds.). The ecology of natural disturbance and patch dynamics.* Academic Press, New York. 472 p.
- CHRISTENSEN, N.L., R. BURCHELL, A. LIGGETT, and E.R. SIMMS. 1981. The structure and development of pocosin vegetation. p. 43-61. *In: Richardson, C.J. (ed.). Pocosin wetlands: an integrated analysis of coastal freshwater bogs in North Carolina.* Hutchinson Ross Publ. Co., Stroudsburg, Pennsylvania. 364 p.
- CHRISTMAN, S.P. and W.S. JUDD. 1990. Notes on plants endemic to Florida scrub. *Florida Sci.* 53:52-73.
- DUEVER, L.C. 1983. Natural communities of Florida's inland sand ridges. *The Palmetto* 3(3):3-5.
- EASTERN SPACE AND MISSILE CENTER. 1989. Weather meteorological handbook ESMC pamphlet 105-1. Department of the Air Force, Eastern Space and Missile Center, Patrick Air Force Base, Florida. 61 p.
- FERNALD, R.T. 1989. Coastal xeric scrub communities of the Treasure Coast Region, Florida. Nongame Wildlife Program Technical Report No. 6. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida. 113 p.
- GAUCH, H.G., JR. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York. 298 p.
- GILL, A.M. and R.H. GROVES. 1981. Fire regimes in heathlands and their plant-ecological effects. p. 61-84. *In: Specht, R.L. (ed.). Ecosystems of the world. 9B. Heathlands and related shrublands analytical studies.* Elsevier, Amsterdam, The Netherlands. 386 p.

- GIVENS, K.T., J.N. LAYNE, W.G. ABRAHAMSON, and S.C. WHITE-SCHULER. 1984. Structural changes and successional relationships of five Florida Lake Wales Ridge plant communities. *Bull. Torrey Bot. Club* 111:8-18.
- HARRINGTON, M.G. 1985. The effects of spring, summer, and fall burning on Gambel oak in a southwestern ponderosa pine stand. *For. Sci.* 31:156-163.
- HARRINGTON, M.G. 1989. Gambel oak root carbohydrate response to spring, summer, and fall prescribed burning. *J. Range Manag.* 42:504-507.
- HILL, M.O. and H.G. GAUCH, JR. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47-58.
- HILMON, J.B. 1968. Autecology of saw palmetto (*Serenoa repens* (Bartr.) Small). Ph.D. dissertation. Duke University, Durham, North Carolina. 190 p.
- HOBBS, R.J. and C.H. GIMINGHAM. 1984. Studies on fire in Scottish heathland communities. II. Post-fire vegetation development. *J. Ecol.* 72:585-610.
- HOUGH, W.A. 1965. Palmetto and gallberry regrowth following a winter prescribed fire. Georgia For. Res. Pap. No. 31. Georgia For. Comm. 5 p.
- HOUGH, W.A. 1968. Carbohydrate reserves of saw-palmetto: seasonal variation and effects of burning. *For. Sci.* 14:399-405.
- HUCKLE, H.F., H.D. DOLLAR, and R.F. PENDLETON. 1974. Soil survey of Brevard County, Florida. U.S. Soil Conserv. Serv., Washington, D.C. 123 p. and maps.
- JOHNSON, A.F. 1982. Some demographic characteristics of the Florida rosemary *Ceratiola ericoides* Michx. *Amer. Midl. Naturalist* 108:170-174.
- JOHNSON, A.F. and W.G. ABRAHAMSON. 1990. A note on the fire responses of species in rosemary scrubs on the southern Lake Wales Ridge. *Florida Sci.* 53:138-143.
- KEELEY, J.E. 1981. Reproductive cycles and fire regimes. p. 231-277. *In*: Mooney, H.A., T.M. Bonnicksen, J.E. Lotan, and W.A. Reiners (eds.). Fire regimes and ecosystem properties. U.S. For. Serv. Gen. Tech. Rep. WO-26. 594 p.
- KEELEY, J.E. and P.H. ZEDLER. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seedling strategies. *Amer. Midl. Naturalist* 99:142-161.
- KRUGER, F.J. 1983. Plant community diversity and dynamics in relation to fire. p. 446-472. *In*: Kruger, F.J., D.T. Mitchell, and J.U.M. Jarvis (eds.). Mediterranean-type ecosystems: the role of nutrients. Springer-Verlag, New York. 530 p.
- KURZ, H. 1942. Florida dunes and scrub, vegetation and geology. *Florida Geol. Surv. Bull.* 23:15-154.
- LAESSLE, A.M. 1942. The plant communities of the Welaka area. *Univ. Florida Publ. Biol. Sci. Ser.* 4:1-143.
- LAESSLE, A.M. 1967. Relationship of sand pine scrub to former shore lines. *Quar. J. Florida Acad. Sci.* 30:269-286.
- MAILANDER, J.L. 1990. Climate of the Kennedy Space Center and vicinity. NASA Tech. Mem. 103498. 62 p.
- MALANSON, G.P. and L. TRABAUD. 1987. Ordination analysis of components of resilience of *Quercus coccifera* garrigue. *Ecology* 68:463-472.
- MALANSON, G.P. and L. TRABAUD. 1988. Vigour of post-fire resprouting by *Quercus coccifera* L. *J. Ecol.* 76:351-365.
- MENGES, E.S. 1990. Twenty years of vegetation change detected by successional vectors for five unburned upland Florida plant communities. *Supp. Bull. Ecol. Soc. Amer.* 71(2):251.
- MUELLER-DOMBOIS, D. and H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York. 547 p.
- MYERS, R.L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine vegetation. *Bull. Torrey Bot. Club* 112:241-252.
- MYERS, R.L. 1990. Scrub and high pine. p. 150-193. *In*: Myers, R.L. and J.J. Ewel (eds.). Ecosystems of Florida. University of Central Florida Press, Orlando. 765 p.

- PROVANCHA, M.J., P.A. SCHMALZER, and C.R. HINKLE. 1986. Vegetation types. John F. Kennedy Space Center, Biomedical Operations and Research Office (Maps in Master Planning format, 1:9600 scale, digitization by ERDAS, Inc.).
- ROBBINS, L.E. and R.L. MYERS. 1990. Seasonal effects of prescribed burning in Florida: a review. Tall Timbers Res. Sta. Misc. Pub. No. 8. 119 p.
- SCHMALZER, P.A. and C.R. HINKLE. 1987. Effects of fire on composition, biomass, and nutrients in oak scrub vegetation on John F. Kennedy Space Center, Florida. NASA Tech. Mem. 100305. 146 p.
- SCHMALZER, P.A. and C.R. HINKLE. 1991. Dynamics of vegetation and soils of oak/saw palmetto scrub after fire: observations from permanent transects. NASA Tech. Mem. 103817. 149 p.
- SWAINE, M.D. and P. GREIG-SMITH. 1980. An application of principal components analysis to vegetation change in permanent plots. *J. Ecol.* 68:33-41.
- TER BRAAK, C.J.F. 1988. CANOCO—a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis. Agricultural Mathematics Group, Ministry of Agriculture and Fisheries, Wageningen, The Netherlands. 95 p.
- TER BRAAK, C.J.F. 1990. Update notes: CANOCO Version 3.10. Agricultural Mathematics Group, Ministry of Agriculture and Fisheries, Wageningen, The Netherlands. 35 p.
- VENO, P.A. 1976. Successional relationships of five Florida plant communities. *Ecology* 57:498-508.
- WEBBER, H.J. 1935. The Florida scrub, a fire-fighting association. *Amer. J. Bot.* 22:344-361.
- WESTMAN, W.E. 1978. Measuring the inertia and resilience of ecosystems. *BioScience* 28: 705-710.
- WESTMAN, W.E. 1985. Ecology, impact assessment, and environmental planning. John Wiley & Sons, New York. 532 p.
- WESTMAN, W.E. and J.F. O'LEARY. 1986. Measures of resilience: the response of coastal sage scrub to fire. *Vegetatio* 65:179-189.
- WHITTAKER, R.H. and G.M. WOODWELL. 1978. Retrogression and coenocline distance. p. 51-70. *In*: Whittaker, R.H. (ed.). Ordination of plant communities. Dr. W. Junk, The Hague, The Netherlands. 388 p.
- WOOLFENDEN, G.E. and J.W. FITZPATRICK. 1984. The Florida scrub jay demography of a cooperative-breeding bird. Monographs in Population Biology 20. Princeton University Press, Princeton, New Jersey. 406 p.

THE BIONETICS CORPORATION
NASA BIOMEDICAL OPERATIONS AND RESEARCH OFFICE
MAIL CODE BIO-2
KENNEDY SPACE CENTER, FLORIDA 32899

Received October 28, 1991; Accepted February 21, 1992.

